# *Diuraphis noxia* and *Rhopalosiphum padi* (Hemiptera: Aphididae) Interactions and Their Injury on Resistant and Susceptible Cereal Seedlings

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**ABSTRACT** Interspecific interactions between the symptomatic (chlorosis-eliciting) Russian wheat aphid, *Diuraphis noxia* (Mordvilko), and the asymptomatic (nonchlorosis-eliciting) bird cherry-oat aphid, *Rhopalosiphum padi* (L.), on four cereal genotypes were examined by simultaneous infestations. Four cereals (i.e., *Diuraphis noxia*-susceptible 'Arapahoe' wheat and 'Morex' barley, and *D. noxia*-resistant 'Halt' wheat and 'Border' oat) and four infestations (i.e., control, *D. noxia*, *R. padi*, and *D. noxia*/*R. padi*) were used in the research. Whereas *D. noxia* biomass confirmed *D. noxia* resistance among the cereals, *R. padi* biomass indicated that the *D. noxia*-resistant cereals did not confer *R. padi* resistance. *D. noxia* biomass was significantly lower in *D. noxia*/*R. padi* infestation than that in *D. noxia* infestation on all cereals, except Border oat, which indicated an antagonistic effect of *R. padi* on *D. noxia*. All aphid infestations caused a significant plant biomass reduction in comparison with the control. In comparison with *D. noxia* infestation, *D. noxia*/*R. padi* caused a significant plant biomass reduction on all cereals, except Morex barley. Although *D. noxia* biomass in *D. noxia*/*R. padi* infestation was significantly less than that in *D. noxia* infestation, leaf chlorophyll reduction was the same between *D. noxia*/*R. padi* and *D. noxia* infestations, which suggested that the asymptomatic *R. padi* enhanced the *D. noxia*-elicited leaf chlorophyll loss. The regression between chlorophyll content and aphid biomass indicated that the asymptomatic *R. padi* in the *D. noxia*/*R. padi* infestation enhanced chlorophyll loss, but interspecific aphid interaction on plant biomass varied among the cereals.

**KEY WORDS** aphid biomass, plant biomass, chlorosis

Different cereal aphids have been known to occupy certain parts of plants both temporally and spatially (Gianoli 1999, 2000). For example, although the symptomatic (or chlorosis-eliciting) Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), colonizes young leaves and elicits chlorosis and leaf rolling, and results in death of young seedlings under severe infestation (Webster et al. 1991, Burd et al. 1993), the asymptomatic (or nonchlorosis-eliciting) bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), prefers mature leaves and leaf sheath of cereal plants (Gianoli 1999), and reduces plant growth. The English grain aphid, *Sitobion avenae* (F.), and *R. padi* have been shown to negatively affect each other's fecundity, although the two species colonize different parts of the wheat, *Triticum aestivum* L., plant (Gianoli 2000). *S. avenae* infests not only the upper mature leaves but also the heads of wheat plants, whereas *R. padi* prefers to colonize the

leaf sheath and lower leaves (Gianoli 2000). When the leaf sheath or the third leaf of the 'Paleta' wheat was infested with *R. padi* for 48 h, a significant reduction in alate fecundity was observed in a subsequent *R. padi* leaf infestation but not on a subsequent stem infestation (Gianoli 1999). The reason that *R. padi* prefers leaf sheath of a plant as its main colonization site might be related to its avoidance of induced responses elicited by previous aphid infestation but not necessarily due to the spatial nutritional value of the plant (Gianoli 1999). In contrast, White (1993) reported that the preference of young (i.e., flush) to old (i.e., senescence) tissue, or vice versa, by an insect herbivore may not necessarily be related to allelochemicals but to the differences in nitrogen nutrients between plant tissues.

Interspecific interactions between aphid species has been examined on a number of host plants, ranging from probiosis (mutual benefit) to antibiosis (suppression) on a given host. The growth of the green spruce aphid, *Elatobium abietinum* (Walker), has been enhanced by previous aphid-infested spruce needles because of its alteration of amino acid balance of the host plant (Fisher 1987). The gray pine needle aphid, *Schizolachnus pineti* F. and the spotted pine aphid, *Eulachnus agilis* (Kaltenback), are mutually benefited by their coexistence on the same host (Kidd

et al. 1985). However, *R. padi* infestation has been shown to negatively affect the development of a leafhopper, *Psammotettix lienus* (Dahlbom), on wheat under both laboratory and field conditions (Alla et al. 2001). Edwards (2001) examined interspecific and intraspecific interactions among three aphid species [the green peach aphid, *Myzus persicae* (Sulzer); the cowpea aphid, *Aphis craccivora* Koch; and the bluegreen aphid, *Acyrthosiphon kondoi* Shinji] on five grain legume hosts [narrow-leafed lupin, *Lupinus angustifolius* L.; faba bean, *Phaseolus vulgaris* L.; field pea, *Pisum sativum* L.; chick pea, *Cicer arietinum* L.; and lentil, *Lens culinaris* Medic.] and found interspecific and intraspecific interactions could influence the results of screening grain legume cultivars for aphid resistance.

Although *D. noxia* and *R. padi* are important pests on cereal production, interspecific interactions are still not well understood. By assessing the influence of consequential infestations of *D. noxia* and *R. padi* on wheat seedlings, Messina et al. (2002) reported that previous *D. noxia* infestation had no effect on subsequent aphid population growth of either species. In contrast, previous infestations of *R. padi* reduced population growth of subsequent infestation of the same species by 50%, but it had no effect on *D. noxia.* Schotzko and Bosque-Pérez (2000) reported that, under the field condition, *D. noxia* resistant wheat did not affect the population dynamics of other aphid species [i.e., *R. padi*, *Sitobion avenae* (F.), and *Metopolophium dirhodum* (Walker)]. Few reports have dealt with the direct interspecific interactions on *D. noxia*-resistant and -susceptible cereal hosts, and their attributions to the chlorosis formation. Because of the agricultural and ecological significance of these aphid species and their cereal hosts, our research focused on understanding the etiological mechanism of cereal aphid-elicited leaf desisting symptom-chlorosis by using a *D. noxia–R. padi* comparative model on *D. noxia*-resistant and -susceptible cereals. Thus, the objective of the present research herein was to compare interspecific interactions and their impact on injury elicitation between *D. noxia* and *R. padi* in simultaneous infestation on four cereals with varying degrees of *D. noxia* resistance.

## Materials and Methods

**Aphid Colony Maintenance.** The colony of *D. noxia* was established originally using aphids collected near Scottsbluff, NE, in 1994, whereas the *R. padi* colony was established using aphids collected near Lincoln, NE, in 1996. 'Stephens' (*D. noxia*-susceptible) winter wheat was used for aphid colony maintenance. Plants were grown in pots (10 cm in diameter) in a mixture of Sunshine soil mix (SunGro Horticulture, Bellevue, WA) and sand (6:1 ratio). Plants and aphids were maintained in Plexiglas cages (30 by 15 by 15 cm) in Percival growth chambers (Percival Scientific, Boone, IA) at 21 ± 1°C, a photoperiod of 16:8 (L:D) h, and 40–50% RH.

**Growth of Cereal Plants.** The four cereals used in the experiment were *D. noxia*-susceptible 'Arapahoe' and -resistant 'Halt' wheat, *D. noxia*-susceptible 'Morex' barley (*Hordeum vulgare* L.), and *D. noxia*-resistant 'Border' oat (*Avena sativa* L.). Arapahoe is a *D. noxia*-susceptible wheat cultivar (Hein 1992), Halt a *D. noxia*-resistant wheat cultivar (Quick et al. 1996), Morex barley a *D. noxia*-susceptible cultivar (Webster et al. 1993), and Border oat a *D. noxia*-resistant oat cultivar (Quisenberry and Schotzko 1994). The influence of leaf epicuticular wax of the four cereals on *D. noxia* probing behavior and nymphoposition (Ni et al. 1998), and oxidative responses of the four cereals to *D. noxia* and *R. padi* feeding (Ni et al. 2001) also have been reported previously. However, the resistance (or susceptibility) of the four cereals to *R. padi* had not been determined. Seeds of Arapahoe and Halt wheat, Morex barley, and Border oat were planted at the rate of three plants per Conetainer [SC-10 Super Cell Single Cell (3.81 cm in diameter by 21 cm in depth) (Stuewe & Sons, Inc., Corvallis, OR)] at the Plant Growth Center, Montana State University, Bozeman, MT. The plants in the Conetainers were placed in the Conetainer racks and kept one space between two Conetainers to provide adequate light. The plants were watered uniformly from the bottom by placing the rack over a plastic tray (54 by 28 by 6 cm) filled with water. Before the initiation of aphid infestation, plants were thinned to one plant per Conetainer. All experimental plants were maintained under the conditions as described previously.

**Aphid Infestation and Data Collection.** At growth stage 13 (i.e., three-leaf stage) (Zadoks et al. 1974), the second leaf of the cereal plants was infested with zero aphids, five apterous adult *R. padi*, five apterous adult *D. noxia*, or five *D. noxia* and five *R. padi* per plant, by using a camel's-hair brush. All control and aphid-infested cereal plants were caged individually using polyethylene tube cages (30 cm in length by 4 cm in diameter) and maintained in a Percival growth chamber under the conditions described above. The experiment was terminated 12 d after the initial infestation. All aphids on the plants were brushed off. Adults and nymphs of *D. noxia* and *R. padi* were separated and weighed on an electronic balance. Because the plants were initially infested with five adult aphids of each species, aphid fresh weight at the end of the experiment was used to estimate its population growth. Although *D. noxia* adults were easily separated from *R. padi* by using body color, the nymphs were separated using body, leg, and cornicle color, shape, and mobility. Although early instars of *R. padi* had greenish color that was similar to *D. noxia*, the nymphs of *R. padi* were more active, and color of cornicles and legs was darker than *D. noxia.* Leaf chlorophyll content of the second leaves from all treatments was measured using a chlorophyll meter (model Spad-502, Minolta, Tokyo, Japan). Three chlorophyll meter readings were recorded on each leaf, and the mean of the three readings was used in data analysis. Leaf chlorophyll content (micromoles per square meter) was calculated according to a standard curve generated for model Spad-502 chlorophyll meter [i.e., chlorophyll ($\mu$mol/m$^2$) = $10^{(M^\wedge \ 0.261)}$],
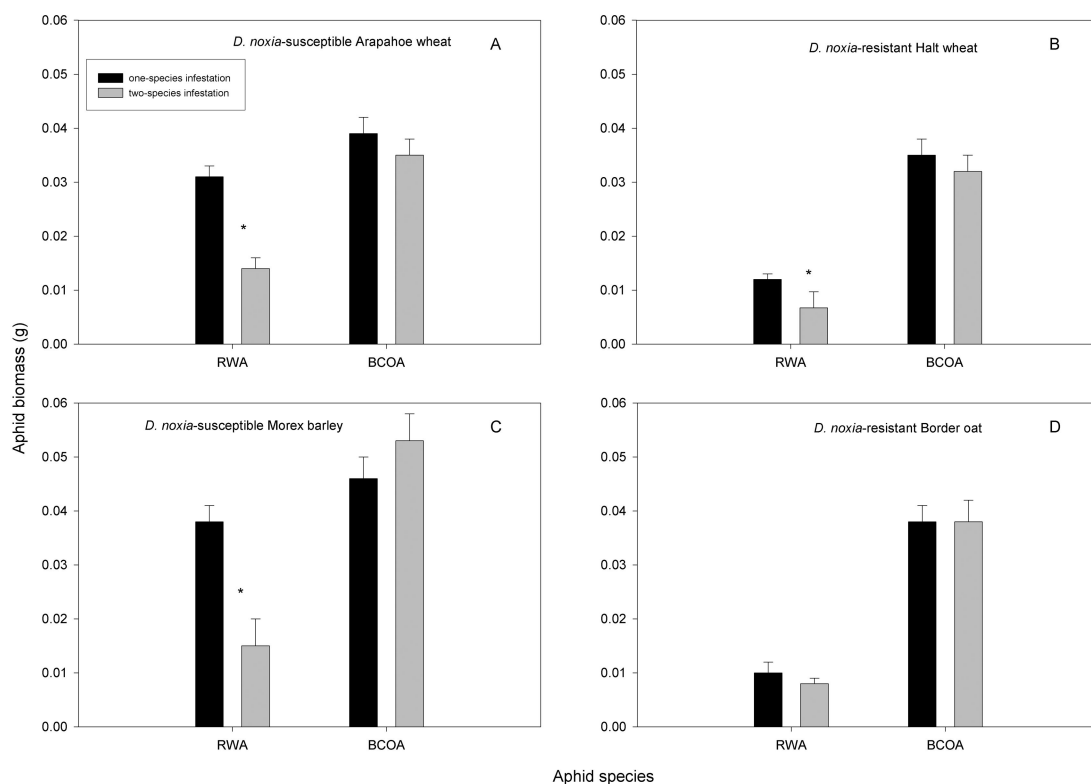
**Fig. 1.** Influence of the single and two aphid species infestations on aphid biomass (grams) on the four cereal genotypes 12 d after the initial infestation. The star denotes a significant difference ($\alpha = 0.05$; pairwise *t*-test) in aphid biomass between single aphid species infestation (dark bar) and two aphid species infestation (gray bar). BCOA, bird cherry-oat aphid (*R. padi*) infestation; RWA, Russian wheat aphid (*D. noxia*) infestation.

where M is the chlorophyll meter reading (Markwell et al. 1995). Each seedling was then excised at the top of the soil and the biomass was recorded using the electronic balance. Because a separate experiment showed that fresh and dry weight of aphids (or plants) had a strong positive and linear correlation (X.N., unpublished data), only fresh weight of aphids and plants were used in the present research.

**Experimental Design and Data Analysis.** We hypothesized that the difference in the combined aphid numbers between *D. noxia* and *D. noxia/R. padi* infestations would not affect leaf chlorosis on all cereals, because the same number (five) of chlorosis-eliciting *D. noxia* was in both types of aphid infestation. The experiment was a two-factor (i.e., four cereals by four aphid infestations as described in the previous subsections) with a completely randomized design. Three plants (or replications) were used per treatment per trial, and six trials were conducted. In total, 18 plants were used for each treatment. The biomass of each aphid species was compared by the pairwise *t*-test between the single and two-aphid species infestations, whereas plant biomass and leaf chlorophyll content were analyzed among the aphid infestations and cereal genotypes by using PROC GLM procedure of SAS software (SAS Institute 1989). The means were separated, respectively, among the four aphid infestations

(i.e., control, *D. noxia*, *R. padi*, and *D. noxia/R. padi* infestations) on each cereal genotype by using the Fisher protected least significant difference (LSD) test ($\alpha = 0.05$). The correlation between plant injury (measured by leaf chlorophyll content and plant biomass) and aphid biomass from *D. noxia*-, *R. padi*-, and *D. noxia/R. padi*-infested four cereal genotypes was analyzed using PROC GLM procedure. The equality of linear regression slopes for *D. noxia* and *R. padi* in *D. noxia/R. padi* infestation was compared using the analysis of covariance (ANCOVA) procedure of the SAS software. The graphs used were generated using SigmaPlot for Windows 8.02A (Systat, Richmond, CA).

### Results

**Aphid Biomass.** Within the three aphid infestation types (i.e., *D. noxia*, *R. padi*, and *D. noxia/R. padi*), *D. noxia* biomass was significantly affected by cereal genotypes ($F = 56.11$; df = 3, 131; $P = 0.0001$), aphid infestation types (i.e., *D. noxia* and *D. noxia/R. padi*) ($F = 99.34$; df = 1, 131; $P = 0.0001$), and the interactions between cereals and aphid infestations ($F = 15.14$; df = 3, 131; $P = 0.0001$). *D. noxia* biomass was significantly higher on Arapahoe wheat and Morex barley (Fig. 1A and C) than on Halt wheat and Border oat (Fig. 1B and D), which confirmed that the latter
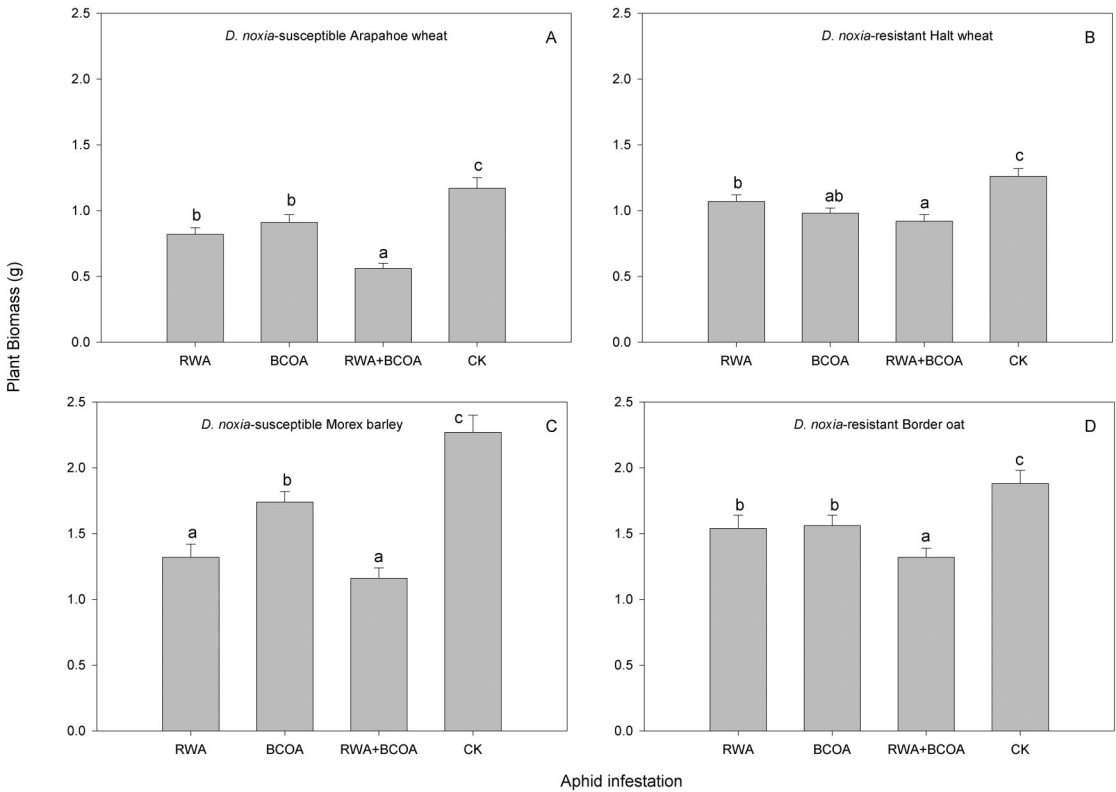
**Fig. 2.** Impact of aphid infestations on plant biomass (grams) of the four cereal genotypes. The bars with different letters denote that significant ($\alpha = 0.05$; LSD) differences among aphid infestations. BCOA, bird cherry-oat aphid (*R. padi*) infestation; CK, control; RWA, Russian wheat aphid (*D. noxia*) infestation.

two cereals were *D. noxia* resistant. The existence of *R. padi* in *D. noxia*/*R. padi* infestation caused significant reduction of *D. noxia* biomass (more than one-half) on susceptible cereals (i.e., Arapahoe wheat [Fig. 1A] [$t = 41.36$, df = 29, $P = 0.0001$] and Morex barley [Fig. 1C] ($t = 41.01$, df = 29, $P = 0.0001$]), whereas the impact of *R. padi* on *D. noxia* on the *D. noxia*-resistant cereals was not conclusive. On *D. noxia*-resistant Halt wheat (Fig. 1B), *D. noxia* biomass from *D. noxia*/*R. padi* infestation was significantly less ($t = 13.23$, df = 31, $P = 0.001$) than biomass from only *D. noxia* infestation; however, on *D. noxia*-resistant Border oat, no *D. noxia* biomass was similar ($t = 3.9$, df = 27, $P = 0.0585$) between *D. noxia* and *D. noxia*/*R. padi* infestations (Fig. 1D).

In contrast, *R. padi* biomass was only significantly affected by cereal genotypes ($F = 19.87$; df = 3, 135; $P = 0.0001$), but not by either the types of aphid infestation or the interactions between cereal genotypes and aphid infestations (all $P > 0.05$). The *R. padi* biomass was the same between *R. padi* and *D. noxia*/*R. padi* infestations ($t = 0.11$, df = 135, $P = 0.7382$). Among the *D. noxia*/*R. padi*-infested plants, *R. padi* biomass on Morex barley was significantly ($F = 6.39$; df = 3, 71; $P = 0.0007$) higher than the other three cereals. Compared with *D. noxia* biomass, *R. padi* biomass was greater than *D. noxia* biomass on all

four cereal genotypes (Fig. 1A–D), which suggested that the cereals were favorable (or susceptible) hosts for *R. padi.*

We consistently observed in all six trials that, in addition to their feeding on lower senescent leaves and leaf sheath, *R. padi* coexisted with *D. noxia* in chlorotic lesions elicited by *D. noxia* feeding on upper young leaves when cereal seedlings were infested with both aphid species. However, we did not observe *D. noxia* coexisted with *R. padi* on either lower senescent leaves or leaf sheath.

**Plant Biomass.** Plant biomass was significantly affected by aphid infestations ($F = 67.78$; df = 3, 266; $P = 0.0001$), cereal genotypes ($F = 131.9$; df = 3, 266; $P = 0.0001$), and the interactions between cereal genotypes by aphid infestations ($F = 6.45$; df = 9, 266; $P = 0.0001$). The aphid-infested plants had a significantly lower biomass than the control plants on all cereals (Fig. 2A–D). Compared with the *D. noxia* infestation, *D. noxia*/*R. padi* infestation caused a significant biomass reduction of Arapahoe and Halt wheat, and Border oat (Fig. 2A, B, and D), but not Morex barley (Fig. 2C). In contrast, compared with the *R. padi* infestation, *D. noxia*/*R. padi* infestation caused a significant biomass reduction of Arapahoe wheat, Morex barley, and Border oat (Fig. 2A, C, and D), but not Halt wheat (Fig. 2B). Although the *D. noxia*/*R. padi*
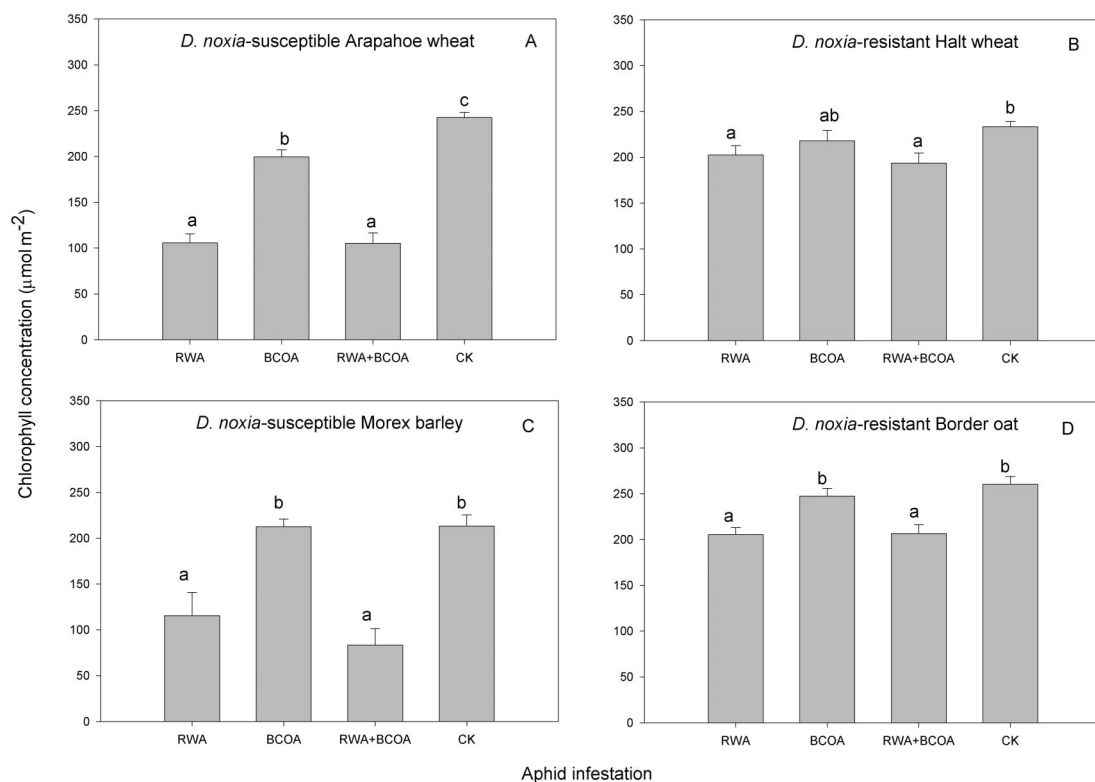
**Fig. 3.** Effect of aphid infestations on chlorophyll content (micromoles per square meter) of the four cereal genotypes. The bars with different letters denote that significant ($\alpha = 0.05$; LSD) differences among aphid infestations. BCOA, bird cherry-oat aphid (*R. padi*) infestation; CK, control; RWA, Russian wheat aphid (*D. noxia*) infestation.

infestation had twice as many aphids (i.e., 10 aphids; five *D. noxia* and five *R. padi*) as the single species infestation (either five *D. noxia* or five *R. padi*) for the initial infestation on all cereals, only Arapahoe wheat and Border oat biomass was significantly lower in the *D. noxia*/*R. padi* infestation than that with either *D. noxia* or *R. padi* infestation (Fig. 2A and D). The biomass of *D. noxia*/*R. padi*-infested Halt wheat was the same as the *R. padi*-infested but less than the *D. noxia*-infested (Fig. 2B), whereas the biomass of *D. noxia*/*R. padi*-infested Morex barley was the same as the *D. noxia*-infested but significantly less than the *R. padi*-infested (Fig. 2C).

**Leaf Chlorophyll Content.** Chlorophyll content was significantly influenced by aphid infestations ($F = 61.28$; df = 3, 265; $P = 0.0001$), cereal genotypes ($F = 39.01$; df = 3, 265; $P = 0.0001$), and interactions between aphid infestations and cereal genotypes ($F = 6.09$; df = 9, 265; $P = 0.0001$). *D. noxia* infestation caused a significant chlorophyll reduction on all cereals in comparison with the control plants (Fig. 3A–D). Although no chlorotic streaks were observed on the *R. padi*-infested plants, a significant chlorophyll reduction was detected on *R. padi*-infested Arapahoe wheat (Fig. 3A) compared with the control plants, but no difference was detected on the other cereals (Fig. 3B–D). Although the biomass of the symptomatic *D. noxia* in the *D. noxia*/*R. padi* infestation was

significantly less than only *D. noxia* infestation on all cereals except Border oat (Fig. 1A–D), no difference (all $P > 0.05$) in chlorophyll content was detected between *D. noxia* and *D. noxia*/*R. padi*-infested plants on all cereals (Fig. 3A–D).

**Correlation of Plant Injury with Aphid Biomass.** Compared with *D. noxia* infestation, low *D. noxia* biomass (Fig. 1) in *D. noxia*/*R. padi* infestation did not alleviate chlorophyll loss elicited by *D. noxia* on 12 d after the initial infestation (Fig. 3). Thus, the correlation between each of the two plant injury measurements (i.e., chlorophyll content and plant biomass) and biomass from both aphid species was examined, respectively, on all four cereals. The slope equality test between the regression lines of the two aphid species was also useful to elucidate interspecific aphid interactions. Only data for the correlation between chlorophyll content and aphid biomass on Arapahoe wheat (Fig. 4A–C) were presented, because the slope equality test of the regression lines in the *D. noxia*/*R. padi* infestation on Arapahoe wheat showed a significant ($P < 0.05$) difference. The data from the other cereals are not presented, because the slope equality tests were not significantly different (all $P > 0.05$). Leaf chlorophyll content was negatively correlated to *D. noxia* biomass on *D. noxia*-infested Arapahoe wheat (Fig. 4A), whereas leaf chlorophyll content was positively correlated to *R. padi* biomass *R. padi*-infested
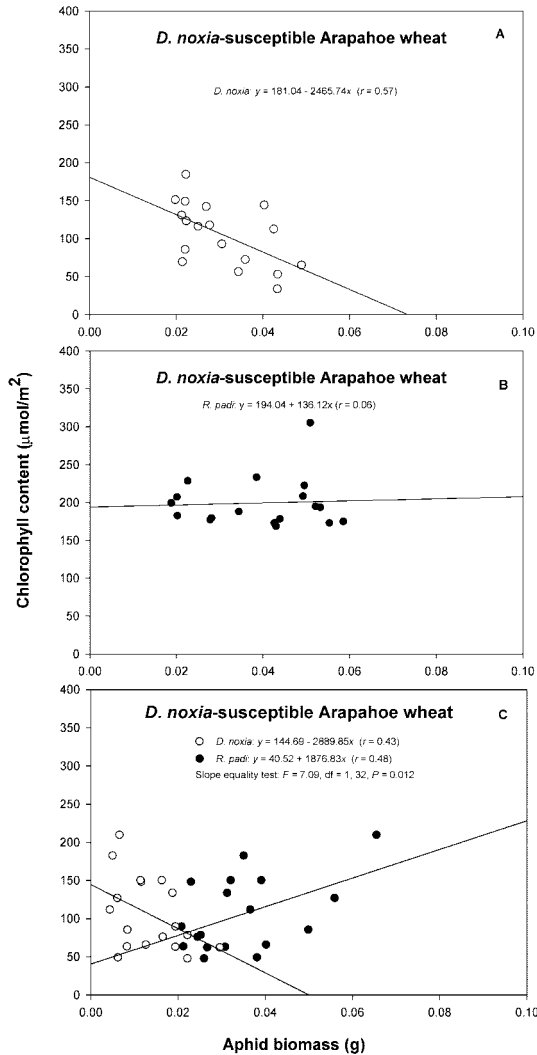
**Fig. 4.** Correlation between chlorophyll content (micromoles per square meter) and aphid biomass (grams) among *D. noxia*, *R. padi*, and *D. noxia*/*R. padi* infestations on Arapahoe wheat.



**Fig. 5.** Correlation between plant biomass (grams) and aphid biomass (grams) among *D. noxia*, *R. padi*, and *D. noxia*/*R. padi* infestations on Border oat.

Arapahoe wheat (Fig. 4B). In the *D. noxia*/*R. padi*-infested Arapahoe wheat plants, the slope equality tests showed that the regression slopes of the two aphid species were significantly different ($P = 0.012$; Fig. 4C) on the *D. noxia*-susceptible Arapahoe wheat, which demonstrated that the coexistence of the two aphid species reduced *D. noxia* population growth, but benefited *R. padi* population growth.

For plant and aphid biomass regression, only data from Border oat were presented (Fig. 5A–C), because a significant ($P = 0.0156$) difference in the slope equality test was detected. The data from the other cereals were not presented, because slope equality tests showed no significant (all $P > 0.05$) difference. The plant and aphid biomass was negatively correlated in either single aphid species infestation on the
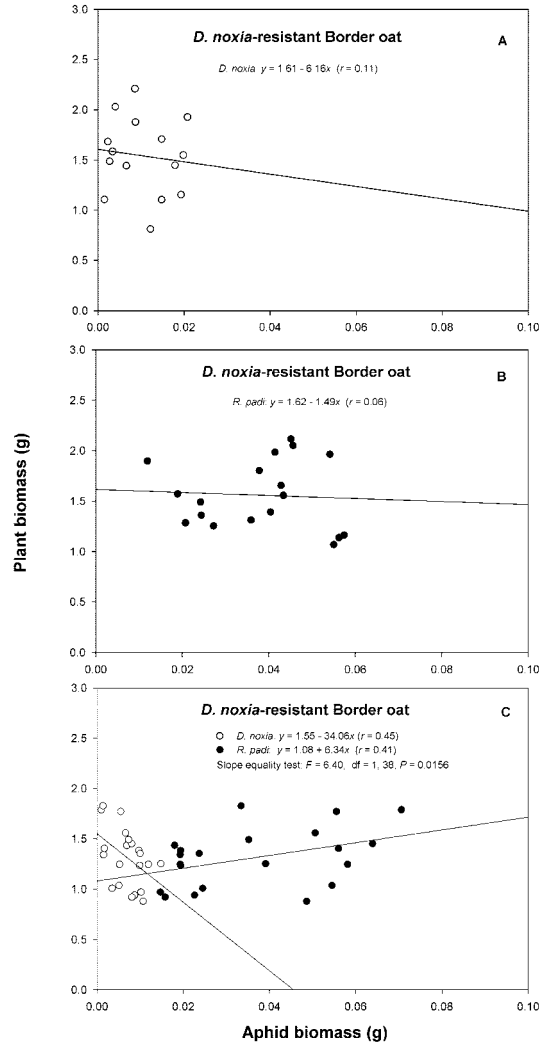
*D. noxia*-resistant Border oat (Fig. 5A and B). However, the regression lines on the *D. noxia*/*R. padi*-infested Border oat showed that plant biomass was correlated to the biomass of the two aphid species oppositely (Fig. 5C). The coexistence of *R. padi* and *D. noxia* negatively affected *D. noxia* population growth, but positively affected *R. padi* population growth.

## Discussion

There are three theories that attempt to decipher intra- and interspecific herbivorous insect interactions mediated by their host plant responses to insect herbivory. The theories are the host defensive response theory (Gianoli 1999, Messina et al. 2002), host nutrient change-engendered herbivore competition theory

(Inbar et al. 1995, 1999; Denno et al. 2000), and the nitrogen availability theory (White 1993). Gianoli (1999) reported that defensive chemicals (e.g., hydroxamic acid) were increased in leaves by prior *R. padi* feeding, which in turn deterred consequent *R. padi* infestation. Aphids in subsequent infestation preferred to feed on leaf sheath and/or stems, but not on the previously infested leaves because of increased defensive chemicals (Gianoli 1999). Messina et al. (2002) reported that although the previous infestation of *D. noxia* on 'Garland' wheat had no effect on the number of either *D. noxia* or *R. padi* in a subsequent infestation, previous *R. padi* infestation caused a significant reduction in the number of *R. padi* in a subsequent infestation, but it had little effect on *D. noxia*. They postulated that such species-specific responses might be the result of specific elicitation of a particular defensive signaling pathway in plants, which modified the impact of aphid feeding on leaf source–sink relationship. The results from the current experiment using simultaneous *R. padi* and *D. noxia* infestations on four cereal genotypes showed that the *R. padi* had an antagonistic effect on *D. noxia*, but *D. noxia* had no negative effect on *R. padi* biomass. This is not consistent with the defensive response theory as described in previous studies.

The host nutrient-engendered herbivore competition theory states that the change in supply of photosynthates was the main cause of the antagonistic relationship between insect species. Using two closely related species of gall-forming aphids (Hemiptera: Pemphigidae: Fordinae), Inbar et al. (1995) demonstrated that *Geoica* spp. feeding on the leaves of *P. palaestina* would cause the death of *Forda formicaria* galls and reduction of reproduction success in surviving galls, whereas *F. formacaria* caused no damage on either *Geoica* spp. reproductive output or its visible injury to pistachio leaves. Several studies of other insects also supports this theory. Other studies have described interspecific interactions of a variety of insects, including interactions between sap-feeding insects (e.g., aphids and leafhoppers) (Moran and Whitham 1990, Salt et al. 1996, Denno et al. 2000, Muller et al. 2001) and between a leafminer, *Liriomyza trifolii* Burgess, and a sap-feeding whitefly, *Bemisia argentifolii* Bellows & Perrings (Inbar et al. 1999). They concluded that the host plant responses to insect herbivory led to asymmetric competition which in turn caused differential population growth of the two herbivores. Thus, the reduction of *D. noxia* biomass in *D. noxia*/*R. padi* infestation in the current study could be explained by the interspecific competition (e.g., crowding) for nutrients and microhabitats on the host plants.

The coexistence of *R. padi* with *D. noxia* in *D. noxia*-elicited chlorotic lesions also could be the result of host plant nitrogen availability. White (1993) found flush feeders often adapt to colonizing young leaves with a relatively high concentration of "readily assimilated nitrogen" in young leaves for "only a short time," whereas senescence feeders adapt to plant tissues with a relatively low amount of nitrogen over

a long period. Flush feeders thrive on vigorous, growing young leaf tissues, but they do not perform well on senescent tissues (White 1993). Although the decrease in allelochemicals and/or increase in other nutrients might have contributed to feeding differences, White (1993) stated that each feeding type had adapted to a different way of life, so that the tissues consumed by one type would not affect the environment of the other type. Several recent reports on cereal aphids have further described aphid-elicited changes in plant nutritional values and nutrient transport abilities. Telang et al. (1999), using collected stylet exudates, determined that *D. noxia* feeding increased the nutritional value of phloem sap from susceptible Arapahoe wheat, but not from resistant Halt wheat. By comparing the impact of three cereal aphid [i.e., *D. noxia*, *R. padi*, and *Schizaphis graminum* (Rondani)] infestations on the nutritional quality of wheat and barley, Sandström et al. (2000) reported that *S. graminum*-ingested phloem sap had a two-fold higher concentration of amino acids and a much higher proportion of essential amino acids compared with that of *R. padi* on both wheat and barley. Effects of *D. noxia* feeding on wheat and barley were similar to *S. graminum*, but much less dramatic (Sandström et al. 2000). In addition, Burd (2002) found that *S. graminum* feeding significantly reduced phloem translocation capability surrounding the feeding site on wheat; however, *D. noxia* feeding showed little impact on nutrient translocation in phloem.

When the regression slopes between *D. noxia* and *D. noxia*/*R. padi* infestations were compared, *D. noxia*/*R. padi* infestation enhanced the negative correlation between chlorophyll content and *D. noxia* biomass on the *D. noxia*-susceptible Arapahoe wheat, although *R. padi* was a nonchlorosis-eliciting species. Also, plant biomass was correlated positively with *R. padi* biomass on the *D. noxia*/*R. padi*-infested Border oat, which differed from a negative correlation shown in the *R. padi* infestation. Thus, the plant and aphid biomass data demonstrated that the coexistence of the two aphid species positively affected *R. padi* population growth but negatively affected *D. noxia* population growth on the *D. noxia*-resistant Border oat. The current study also demonstrated that there was no correlation between *D. noxia* and *R. padi* resistance on the four cereal genotypes. The finding corroborates the results of Schotzko and Bosque-Pérez (2000) that, under the field conditions, wheat genotypes with varying *D. noxia* resistance had no effect on *R. padi* population dynamics.

We conclude that compared with single species infestation, *D. noxia*/*R. padi* infestation showed no negative effect on *R. padi* biomass but suppressed *D. noxia* biomass. However, low *D. noxia* biomass did not alleviate leaf chlorosis, which could be the result of interspecific aphid interactions. Our findings supported the nitrogen availability theory. The correlation between plant injury and aphid biomass indicated that the *D. noxia*/*R. padi* infestation affected leaf chlorophyll and plant biomass differently. The interactions between the two aphid species merit fur-

ther study by using a series of aphid infestation levels (e.g., 0, 5, 10, and 20) for both single- and/or two-species infestations to unravel the mechanism of *D. noxia*-elicited leaf chlorosis as well as interspecific interactions between the two aphid species.

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